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THE SPIROCHETES AND THEIR RELATIONSHIP TO OTHER ORGANISMS

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IN Ehrenberg's famous work, "Die Infusionstierchen als vollkommene Organismen," written in 1838, the fourth family of the Vibrionides, or vibrating animalcules, includes five genera which that author regarded as animals and distinguished as follows:

Segmented threads (monad-stocks)
- rectilinear (by rectangular transverse fission)
  - non-flexible .... *Bacterium*
  - serpentine and flexible .. *Vibrio*
- spirally twisted (by oblique transverse fission)
  - twisted segments
    - flexible .... *Spirochæta*
    - inflexible
      - cylindrical elongate *Spirillum*
      - discoidal compressed *Spirodiscus*

The details of structure which Ehrenberg had elsewhere worked out with too imaginative industry, he sadly acknowledges are here "barred to our present powers of vision by virtue of their minuteness"; and he is forced to depend upon scanty data to differentiate the to him closely related genera. To-day three among the associated genera are generally recognized as bacteria and of the spirochetes alone is there doubt as to their proper relationship in the systematic tree.

However, Ehrenberg was not the first to observe such organisms. In 1773 O. F. Müller described corkscrew-like animalcules found in foul water, and in 1786 discussed and figured several species, unconscious that in 1777 Köhler had published the first figure of such a form.

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[1] Studies from the Zoological Laboratory, The University of Nebraska, under the direction of Henry B. Ward. No. 90.

Yet both descriptions and figures are far too indefinite to permit of more than a guess as to the genus under consideration. Even Ehrenberg's work affords scanty means for the recognition of the forms of which he listed one spirochete and three spirilla. The group, though familiar to all students of microscopic life, has remained only superficially known up to very recent times, in fact until the discovery of the important rôle which certain of them play in the production of disease turned once more the attention of investigators in this direction. Despite the characteristic of flexibility noted by Ehrenberg, and the indifference they displayed towards ordinary methods of bacteriological culture, most authors have grouped these organisms together among the bacteria. Renewed attention to the group served to emphasize at once radical differences of opinion as to its interpretation.

Undoubtedly the impetus to this study was given by Schaudinn's discovery of such an organism in syphilis and the intuitive inference which has been abundantly verified that others would be found in similar relation to diseases as yet entirely unexplained. Working on this and on other species, Schaudinn confirmed the view of Ehrenberg as to the characteristic flexibility of the spirochetes, and determined the occurrence of longitudinal division and the presence of polar flagella, single save just before division. He also demonstrated certain differences between the form found in syphilis and other common spirochetes, which he thought served to justify their generic separation. Throughout he maintained firmly the animal nature of the group.

Almost simultaneously there appeared in 1906 several papers which dealt with the problem as to the nature of this group and arrived at diametrically opposite conclusions. In the first, by the parasitologist Blanchard (1906), was analyzed briefly the morphological basis for the genera of microorganisms in which the body has the form of a spiral. In comparison with these the author considered very briefly also certain clearly bacterial forms (*Spirosoma, Vibrio, Spirobacillus*) and others distinctly flagellate (*Trypanosoma, Trypanoplasma*) which in his opinion manifest close relationship to the true spiral microorganisms of which he recognized three well-founded genera, *Spirillum, Spirochæta* and *Treponema.* The group of plant organisms he classed as follows:

SPIROBACTERIA Cohn 1875

Bacteria more or less curved in a spiral, the curve forming at times only the arc of a circle, in other cases forming spiral coils more or less numerous. Organisms little flexible or not at all, multiplying by transverse division. Formation of endogenous spores demonstrated in a number of species.

Four genera: *Spirosoma, Vibrio, Spirobacillus, Spirillum.*

Of the last genus he says: *Spirillum* Ehrenberg 1830—Body spiral, cylindrical in transsection, not tapering at the ends. No undulating membrane. One or several flagella bent in a regular curve, either at both extremities or at one only. Formation of endogenous spores demonstrated in a number of species. Organisms relatively of considerable size, cultivated easily on various media used in bacteriology.

The spirilla are clearly bacteria. They live as saprophytes in wells, stagnant waters, the soil, liquid manure, etc., and generally in media very poorly oxygenated. Possibly one should include in this genus some forms which are found in pus, but it is doubtful if these play an active part in it, and up to the present time not a single species can be considered as surely pathogenic.

Over against these forms, and sharply contrasted with them Blanchard placed the animal organisms of a general spiral form. These he included in a single family, characterized thus:

TRYPANOSOMIDÆ Doflein 1901

Flagellates twisted into a spiral, the coils being more or less numerous. Organisms flexible, with form more or less fixed, multiplying by longitudinal division. No endogenous spores. Locomotive apparatus consisting either simply of an undulating membrane, or of such a membrane together with one or two flagella. Not stained by Gram's method, not cultivated in the media used in bacteriology.

Four genera: *Spirochæta, Treponema, Trypanosoma, Trypanoplasma.*

The first two genera are very similar and include the only forms concerning the animal nature of which there is any question. It will be necessary to consider these somewhat closely. The first is characterized thus:

SPIROCHÆTA[1] Ehrenberg 1833

Body excessively slender, spiral, flattened, ectoplasm extending in a narrow undulating membrane which surrounds in a spiral the entire body. No flagella, no endogenous spores. Nucleus greatly elongated, filiform, in the axis of the body, with chromatin granules distributed along its surface. Reproduction in all probability by longitudinal division. None of the media used in bacteriology serve to maintain cultures of these organisms. Type species, *S. plicatilis.*

All these forms are by some students assigned to the bacteria. Some species are inhabitants of stagnant waters, others live in the sea or in decaying organic materials, while still others are parasitic. Among the latter are forms recently recognized as the cause of most virulent infective diseases in man and other animals. The genus characters given above are not in their original form, but as emended by Blanchard, and this emendation becomes now the basis of the group thus named. The emendation is based primarily upon the epoch-making investigations of Schaudinn.

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[1] The name is often written *Spirochæte,* which does not conform to rules of Latin or of nomenclature.

Blanchard lists in this genus the following species:

1. *S. plicatilis* Ehrenberg 1833, from stagnant water.
2. *S. buccalis* Cohn 1875, from the buccal cavity.
3. *S. obermeieri* Cohn 1875, from the blood of man in cases of relapsing fever. The possible varieties of this species, found in various types of relapsing fever, are also noted.
4. *S. dentium* Koch 1877, very small species from the mouth.
5. *S. gigantea* Warming 1875, from brackish water.
6. *S. eberthi* (Kent 1880), from the intestine of birds.
7. *S. balbianii* (Certes 1882), from the intestine of lamellibranchs.
8. *S. anserina* Sakharov 1891, cause of septicemia in birds.
9. *S. theileri* (Laveran 1903), from blood of cattle.
10. *S. pyogenes* (Mezincescu 1904), from pus in a case of pyelitis.
11. *S. gallinarum* R. Blanchard 1905, cause of septicemia among chickens.
12. *S. refringens* Schaudinn 1905, from lesions of syphilis.
13. *S. pertenuis* Castellani 1905, from lesions of yaws.
14. *S. ovina* R. Blanchard 1906, from blood of sheep.
15. *S. vincenti* R. Blanchard 1906, from abscesses in man.

Also several other uncertain forms.

It is evident that this assemblage of forms is not entirely natural. Of many little is known beyond the size and manner of life. The latter presents radical differences, but the formation of new genera on purely physiological grounds is recognized as a most dangerous procedure. No doubt better knowledge, especially of the life cycles, will lead to the removal of groups of these species to new genera, but such must be based upon distinctive characteristics; any other method only results in greater confusion. New forms are being described constantly, *e. g.*, *S. lymphatica,* which White and Proescher regard as the cause of a lymphatic spirillosis; it stains like *Treponema pallidum.* More extended investigation alone will justify assigning a definite place to such organisms. Yet apparently the group of spirochetes producing relapsing fevers may justly be made an independent genus, even though their morphological differentiation is difficult. They constitute the newly created genus.

SPIROSCHAUDINNIA Sambon 1907

Blood parasites only imperfectly known. In blood of vertebrate host, they appear as minute, wavy or spiral threadlike bodies. With undulating membrane but no flagella. Free stage alternates with intracellular resting stage with parasite coiled up in host cell. Sporogony in ticks. Stages have been demonstrated in ova, showing the hereditary transmission of the infection. This is contrary to known facts regarding bacteria. Type species, *Spiroschaudinnia recurrentis.*

This genus is as yet not clearly differentiated from *Spirochæta* and may ultimately prove to be synonymous with it. The presence of an intracellular stage and the mode of infection through biting insects are the slender basis on which it rests at present.

In this genus Sambon has included two forms which produce relapsing fevers in man. One is *S. recurrentis* (Lebert 1874), better known by the synonym *Spirillum obermeieri* Cohn 1875, which is the cause of the relapsing fever common in Russia, the Balkan Peninsula, Turkey, Persia and India, and known by sporadic cases over the entire world. Patton has shown that the parasite is transmitted by the common bedbug (*Acanthia lectularia*) and possibly by the body louse (*Pediculus vestimenti*), although the evidence is not conclusive. The second species, *S. duttoni,* the cause of African relapsing fever, is difficult to distinguish morphologically from the foregoing, but is shown by experiment in animals to be distinct from it. According to Dutton and Todd the organism is transmitted by the tick, *Ornithodoros moubata*

(Murray). The young of infected ticks are capable of inoculating the disease and the spirochætes have been found in the eggs, where in fact they multiply and thus infect the new generation. This is evidently true hereditary transmission of disease.

A third species should be added to this genus, namely, the organism producing the relapsing fever of Bombay which Novy and Mackie have shown by inoculation experiments to be distinct from either of the preceding forms. To this form the name *Spiroschaudinnia carteri* has recently been given by Mackie. The disease caused by this species has been transmitted experimentally by a grooved needle and also by the bedbug, and none of the experimental animals contracted the disease in any other way than by inoculation.

In his outline Blanchard included one other genus, which with its diagnosis is as follows:

TREPONEMA Schaudinn 1905

Spiral body not flattened, but cylindrical in transsection, tapering towards the extremities. One flagellum at each extremity, no undulating membrane. Multiplication by longitudinal division, the initial stage of which may be identified by the doubling of the flagellum at one of the ends. Division forms remain long attached by their ends. Type species; *T. pallida*. One of the marked characteristics of this spirochete is the resistance to ordinary methods of staining. This stands in sharp contrast to conditions among bacteria. Gram's method and many others do not stain it at all, while no stain colors it deeply.

This form was discovered by Schaudinn and Hoffmann in syphilitic lesions; it has been experimentally transferred to apes, with the result of producing characteristic signs of the disease and has not been found in other diseases. Another species, *T. pertenuis* (Castellani 1905), which is regularly associated with the tropical disease known as frambœsia, or yaws, also belongs here.

But even after these forms have been removed Blanchard's original list of the genus *Spirochæta* still shows an unnatural mixture of varied forms. Among the remaining species are undoubtedly those which form other natural groups and will later be assigned to new genera; but in the absence of fuller knowledge they may preferably be left for the present in the old genus. No doubt new forms will be added to this list. In this connection attention should be called to yellow fever and the view often expressed that the yet unknown cause of this disease will also prove to be a spirochete. Similarly the Miana disease of Persia known to be transmitted by a bird tick, Argas persicus, and other tick diseases in tropical and subtropical countries are thought to be due to the inoculation of closely related organisms.

Only two weeks later than the publication by Blanchard appeared an extensive paper by Novy and Knapp (1906). These authors recorded studies on a spirochete from a case of relapsing fever which was observed in Bellevue Hospital, New York. They regarded this form as identical with *S. recurrentis* and as the result of most careful studies reached the conclusion that the organism in question was undoubtedly a bacterium and not a protozoon. Their figures show strong evidence of transverse division and fail to indicate any trace of bodies which might be interpreted as nucleus, blepharoplast, or undulating membrane. They indicate also the presence of a single flagellum at one end of the spiral about as long as the spiral itself and with wavy turns corresponding in general to those of the spirochete, while a short process occurs at the other end. The staining qualities of the flagellum, the action of the organism under the influence of plasmolytic changes, its behavior both during and after being killed by heat and also the persistence of the spiral form under the most varied injurious conditions, are incompatible, in their opinion, with a protozoan nature and indicate affinity to the bacteria. The readiness with which these authors established active immunity is offered as additional proof of the bacterial nature of the form with which they experimented, and finally they record the absence of a tendency to form layers around each air bubble, which is a very characteristic reaction for trypanosomes. Novy and Knapp conclude thus:

> "The several facts which have been brought out under the preceding headings point clearly to the non protozoal nature of *S. obermeieri*. We must conclude, therefore, that the *S. obermeieri* belongs to the bacteria and more especially to the Spirillaceæ. As pointed out, the same conclusion has been reached by Borrel as regards *S. gallinarum* and *S. duttoni*. Three typical spirochetes are therefore demonstrated to belong to the group of bacteria.
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> "Hitherto it has been assumed that insect transmission indicates a protozoal organism, and in so far as the spirochetes are concerned, the chief evidence which can now be adduced in support of their animal nature is the fact of such transmission in the case of *S. duttoni* and *S. gallinarum*. The facts brought out in this study point so conclusively to the bacterial nature of the organisms that there can be little or no doubt of the correctness of the conclusion arrived at. With the recognition of this proof it follows that insect transmission is no longer a criterion of the nature of an organism."

Radical as is this critique of the animal theory of spirochete relationship, it has not been accepted as deciding the question, and has only provoked further discussion of the problem. Referring first to the question of insect transmission, it may be said that Koch has shown that the spirochetes multiply in the eggs of ticks and Carter that they undergo there changes as yet unexplained which may substantiate the claim of another cycle. Several investigators have found that in experimental animals they pass through the placenta from the maternal circulation to the fetal, although they undergo no changes consequent to this transfer. These observations do not accord with known facts concerning other bacteria.

Almost at the same time there was published an exceedingly careful investigation into the structure and development of the fowl spirochetes by Prowazek, with an appendix on a species from *Anodon* by Keysselitz, in which both authors come to conclusions diametrically opposed to those of Novy and Knapp with regard to the structure and relations of the spirochetes. It should be remembered that the species (*S. gallinarum*) on which Prowazek worked was one of those which Novy regarded as most positively of plant affinities. On the basis of most critical observations Prowazek indicates the presence of an undulating membrane with a conspicuous marginal cord. The body of this spirochete he finds to be flexible, a feature emphasized by various authors in the diagnosis of the genus. An analysis of the various types of movement shows, in his opinion, marked similarity to organisms possessing an undulating membrane or to the similarly provided sperm cells. Distinct granules lie in the axis of the organism which do not constitute a definite nucleus in the general sense of the term, but form chromidia such as are well known to occur frequently in the protozoon cell in the place of a single circumscribed nucleus.

So far as the conduct of these spirochetes towards reagents is concerned, the use of salt solutions did not produce the plasmolysis characteristic for bacteria even though the solutions were stronger than those sometimes successful in effecting this among the bacteria. Dilute alkaline solutions affected the spirochetes whereas the bacteria are very resistant towards them.

The identification and interpretation of the method of division is believed to be of especial importance in determining the systematic position of the spirochetes. In the opinion of Prowazek transverse division may occur, yet positive evidence demonstrated the occurrence of longitudinal division. Similar conditions in part were found on the species from the mouth (*S. dentium*), and were especially clearly illustrated by the observations of Keysselitz on a spirochete obtained from the fresh water mussel. Here the character of the undulating membrane and of the chromidia, the conduct of the chromatin granules in advance of division and the essential features of that process which was clearly longitudinal could be most distinctly observed and delineated. Finally Prowazek calls attention to various protoplasmic accumulations or globules which make their appearance at certain times and in his opinion are not mere products of regeneration, but represent special resting stages in which protoplasm and chromatin granules experience involution. These peculiar processes have also been observed by other investigators on other species and may possibly be interpreted as particularly related to the sexual cycle.

Prowazek concludes that as regards the systematic position of the chicken spirochete (*S. gallinarum*), one is compelled on the basis of the structure, relation to reagents, manner of plasmolysis, and also on the basis of temporary cell parasitism to place the species among the protozoa and in close proximity to the trypanosomes. The undulating membrane was observed by Schaudinn in *S. dentium, refringens* and *ziemanni.* The existence of this structure can no longer be questioned. The large form discovered by Keysselitz suggests the large *S. plicatilis* and forms the transition to *S. balbianii* of the oyster which is without doubt closely related to the trypanosomes.

In a very recent paper Fantham (1908) demonstrates the occurrence and character of the spiral membrane in *S. balbianii* and *S. anodontæ.* He also explains the character of the movement as due to myonemes in the spiral membrane. Longitudinal division he finds to be frequent and to involve first the basal granules, then the membrane, next the chromatin masses and finally the body, the halves of which subsequently remain attached end to end. Fantham sees no clear evidence of sexual dimorphism, and finds the spirochætes non-plasmolyzable and without aerobic reactions. As characters manifesting bacterial affinities he lists the diffuse nucleus like spirilla; transverse fission even though infrequent, and the absence of a blepharoplast. Features suggesting protozoan affinities are the possession of a membrane, longitudinal fission, their non-plasmolyzable character and several minor or doubtful factors. The spirochetes he believes to be distinct from trypanosomes in their less highly specialized structure, which exhibits morphological resemblance to bacteria.

In the face of such conflicting testimony on these morphological and physiological factors of primary importance for the interpretation of the group, one is compelled to seek collateral evidence to see if any can be secured which is definite, even though not in itself decisive. A few such indications are to be found among the uncontroverted records of various investigators. It is noteworthy that spirochetes resist culture in the media which serve readily for bacteria in general, and herein also resemble other protozoan saprozoites.[2]

Among indirect evidence one should note the work of Marchoux.[3] It has been observed that spirochetes easily lose their virulence. This author found that *S. gallinarum,* if passed through a series of birds, loses its lethal power and infectivity. In nature, however, the disease maintains its virulence, destroying entire broods in countries where it is endemic. The persistent virulence is thus seen to be related to the transmitting agent, the tick *Argas miniatus.* However, these ticks are incapable of increasing the virulence of a strain that has become attenuated and merely maintain any strain at its own level. These conditions do not resemble the action of bacteria, but, on the other hand, do simulate the conduct of protozoa, which pass through part of the life cycle in an intermediate host.

Another indication of much importance was furnished by Lingard in 1903 when he observed spirochetes in cattle penetrating red blood cells. Prowazek describes and figures in detail this occurrence in the fowl's blood where the parasite, after entering the corpuscle assumes a coiled or resting condition which he believes related in some manner to the (supposed) developmental cycle in the intermediate host (*Argas*). Very recently Balfour (1907) has seen the spirochete actually enter the red corpuscle, and undergo changes within it in which the chromatin core is broken up into separate globules. This stage is very difficult to stain and has hitherto escaped emphasis. Some observers believe it to represent degeneration changes; even then it is incompatible with the theory of bacterial relationship, while, on the other hand, it suggests strongly conditions which prevail among other hematozoa. One is forced to note its great resemblance to the "latent body" of trypanosomes recently described by Moore and Breinl. This consists of a nucleated fragment of protoplasm which is stored up in spleen and bone marrow of infected animals and ultimately reappears in the circulation when it gives rise to a new trypanosome.

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[2] This convenient term introduced by Blanchard indicates at sight its meaning through analogy with the well-known botanical term, saprophyte.

[3] *C. R. Soc. Biol.,* 62, October 12, 1907.

Jaffé (1907) has studied a form (*S. culicis*) found in mosquito larvæ and gives a careful analysis of the motile phases which stand in sharp contrast with the stiff screw movements of spirilla. He emphasizes also the ribbon-shaped body, the great susceptibility to solution of KOH even though very dilute, the axial nuclear (?) thread, and the occurrence of both transverse and longitudinal division.

The last work by Dutton and Todd (1907) demonstrated for *S. duttoni* a ribbon-shaped body with a central deeply staining core and a lighter periplastic sheath which at one end at least is prolonged into a flagellum. The central core does not stain uniformly, but has unstained areas and is sometimes broken up into granules. While these organisms occur singly, chains of three or four are frequent. They usually multiply by transverse fission, but longitudinal division also occurs periodically. Many forms taken from spleen and bone marrow are tightly coiled and a few of these undergo remarkable changes there. In the tick involution changes were observed including fragmentation of the chromatin. This process takes place in the Malpighian tubules where apparently, the bodies burst and the granules become free to form the starting point for a new generation.

The group is evidently a doubtful one even yet. The occurrence of chains and of transverse division strongly favors a bacterial interpretation, but on the whole the trend of recent investigation has been to indicate its protozoan affinities and away from the earlier view of bacterial relationship. The spirochetes are certainly distinct from the spirilla and whether they are ultimately placed among bacteria or protozoa, it seems clear that they will occupy a more isolated position than has previously been assigned them by the advocates of either view. On the other hand, the recent proposal of Fantham to create for them a new group, the Spirochætacea, midway between the protozoa and the bacteria, can not be regarded as a helpful move. Such proposals in other groups have been found on later study to be evidence of an insufficient knowledge of the forms under consideration. Further investigation into the life history will undoubtedly furnish the definite evidence for a decision of the question.

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